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The Coprophilous Fungal Community: An Experimental System

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INTRODUCTION

In an earlier review (Wicklow, 1981a) I attempted to show how coprophilous fungi provide model systems for studying the organization and function of naturally occurring fungal communities and for examining interactions among decomposer functional groups.

Dung substrates are the equivalent of sinking 'islands' on which the fungal colonists (vegetative cells) are doomed as the dung decomposes and becomes incorporated into the soil. Fungi that fail to fruit and discharge spores cannot escape from the dung and may become locally extinct. It is therefore critical that coprophilous fungi disperse efficiently to reach and colonize fresh substrate. Many coprophilous fungi rely almost entirely on a cyclic process involving herbivore ingestion of spores with foliage, germination of spores following passage through the gut, mycelial growth within dung and eventual sporulation thereon, and dispersal of spores to herbage. Frequently violent phototrophic spore discharge may shoot spores great distances (Webster, 1970). Some coprophilous fungi are carried to fresh dung by arthropods (see Malloch and Blackwell, this volume). Since coprophilous fungi depend entirely on spores as a means of escaping from spent fecal substrate and reaching fresh substrate, sporocarp production (reproductive success) is a relevant measure of fitness.

Dung resource units (pellets or pats) comprised of equivalent numbers and kinds of fungal species can be easily prepared and handled as experimental units. Vegetation harvested from the field can be fed to animals in pens or cages. The dung produced by these animals will contain spores of coprophilous fungi that contaminated the vegetation (Wicklow and Moore, 1974; Wicklow et al., 1980a; Yocom and Wicklow, 1980) Alternatively, different species of coprophilous fungi can be added, as spores, to commercial, pelletized rabbit ration (Harper and Webster, 1964; Wicklow and Yocom, 1981; Kuthubutheen and Webster, 1986b). Harper and Webster's experimental approach has proven ingenious because it allows one to experimentally construct different fungal com-

munities while preserving the structural integrity of the dung as well as the naturally occurring bacterial microflora.

Given these options, experiments can be conducted in the field or under controlled laboratory conditions, and the response of fungal populations compared directly. Dung provides all of the nutrients necessary to support the growth and sporulation of individual species comprising the coprophilous fungal community. Therefore, variation in the resource quality of the habitat in which dung is deposited will not directly affect the ability of coprophilous fungi to grow and produce spores. A plant or animal ecologist would have considerable difficulty in effectively duplicating such experiments in aquatic or terrestrial ecosystems without substantial destructive or artificial manipulation of the biotic communities.

The use of semi-natural 'copromes' in ecological studies with coprophilous fungi is described by Safar and Cooke (1988b). Pelletized copromes are prepared from powdered rabbit dung sterilized by gamma-irradiation. Individual copromes are inoculated with a fungal spore suspension and incubated in a moist chamber. Fungal biomass (chitin-glucosamine assay), sporocarp production, and losses in coprome dry weight can be determined at regular intervals. Copromes should prove useful in studies of the abilities of individual coprophilous fungi or bacteria to chemically alter the dung, release nutrients, and affect weight loss. However, as pointed out by Cooke and Safar (1988b) evaluations of fungal growth or sporulation on copromes in the absence of bacterial populations are less relevant to the natural situation.

In my earlier review I suggested that ascospore color mutants might offer a means of measuring the performance, in situ, of individual genetically altered fungal strains (Wicklow, 1981a). Webster (1970) reported that when wild-type black ascospores of *Sordaria fimicola* and ascospores from a "melanin-free" white- spored mutant were mixed together on pelletized chow that was fed to a caged laboratory rabbit, hybrid perithecia containing both white and black ascospores were observed on the rabbit's feces. An approximate measure of the relative gain or loss in fitness attributed to selected biochemical attributes might be estimated by determining ratios of wild-type versus color mutant spores. In the last decade molecular genetics has provided tools enabling much greater precision in eliminating the production of specific degradative enzymes or in blocking a biosynthetic pathway. At the same time, coprophilous fungi have provided numerous model systems for genetic, biochemical and molecular studies [e.g. *Ascobolus immersus* (Meinhardt et al., 1984); *Ascobolus stercorarius* (Bistis and Raper, 1963); *Coprinus cinereus* (May, 1988); *Cyathus stercoreus* (Lu, 1964); *Podospora anserina* (Schulte et al., 1988); *Podospora curvicolla* (Bockelmann and Esser, 1986); *Sordaria fimicola* (El Ani and Olive, 1962); *Sordaria macrospora* (Esser and Straub, 1958)]. Only the cactophilic yeasts (Starmer et al., 1982; Lachance et al. 1988) may provide as much basic information about the genetics and biology of a saprobic fungal community.

SUBSTRATE SPECIALIZATION

Many coprophilous fungi are found associated with one or a few types of dung (Mitchell, 1970; Lundqvist, 1972; Richardson, 1972; Angel and Wicklow, 1975; 1983; Wicklow, 1981a; Abdullah, 1982). When a caged rabbit and sheep were fed hay from the same bale, different fungal species were recorded on the dung produced by these animals (Wicklow et al., 1980a). There is little or no experimental data to explain fungal 'preference' for a given dung type. For example, no one has determined if the tex-

ture or chemical composition of dung affects fungal colonizing-ability or fruiting. Fungal species found on one dung type may exclude potential competitors common to other dung types. There is an obvious need to contrast the survival and germination of fungal spores that have passed through the guts of different herbivores.

The spores of some coprophiles may be activated by extractable products in the herbivore digestive tract. One method used to trigger spore germination in coprophilous fungi consists of suspending spores in sterile alkaline pancreatin (pH 9.5) at 37°C for 5 hours (Safar and Cooke, 1988a). *Saccobolus versicolor* ascospores germinated following the addition of 0.2% KOH to the surface of agar inoculated with spores (Kuthubutheen and Webster, 1986b). Sporangiospore germination in *Pilobolus crystallinus* was stimulated by the filtered washings of stomach lining from a deer (Morinaga et al., 1981). In this example, germination rates exceeded those recorded for deer dung extract or distilled water controls. The authors suggest that *Pilobolus crystallinus* spores germinate in deer stomachs. Kuthubutheen and Webster (1986b) found no germinated spores of eleven coprophilous fungi in freshly voided rabbit dung by direct microscopic observation of spores in macerated dung.

Culture filtrates of *Bacillus* spp. and *Streptomyces* spp. stimulated sporangiospore germination in *Pilobolus crystallinus*, while filtrates of several fungal cultures gave germination rates similar to the dung extract or distilled water controls (Morinaga et al., 1981). The authors suggest that some dung microbes produce coprogen-like porphyrins which trigger spore germination. Hesseltine et al. (1953) identified coprogen (Pidacks et al., 1953), as a substance essential for the growth of *Pilobolus* spp., and extracts of different types of herbivore dung varied in their ability to stimulate sporangial production in *Pilobolus crystallinus* and *P. kleinii* (Singh and Webster, 1976). By contrast, *Pseudomonas paucimobilis* isolated from rabbit dung inhibited germination of *Pilobolus crystallinus* spores on rabbit dung agar and also prevented sporangium production on autoclaved dung pellets (Anson et al., 1985). Furthermore, bacteria or their culture filtrates caused significant reductions in ascospore germination on dung extract cellulose agar, but did not prevent the establishment of mycelia within copromes (Safar and Cooke, 1988b).

Naturally occurring chemicals in dung have been shown to trigger spore germination. Free phenolic compounds with substitutions only at the para-position in the ring are effective in activating dormant ascospores of coprophilous fungi at concentrations of 1×10^{-4} to 1×10^{-3} M (Furuya and Naito, 1980). The effective compounds included phenol, hydroquinone, p-fluorophenol, p-chlorophenol, p-bromophenol, p-iodophenol, p-cresol, p-phenolsulfonic acid and p-hydroxybenzaldehyde. Furuya and Naito suggest that herbivore-ingested plant phenolic compounds may serve to activate ascospore germination in the coprophilous Sordariaceae. Ascospores of *Sporormiella intermedia* germinated after exposure to 0.001% furfuraldehyde followed by heat (60–65°C) for 30 min. (Kuthubutheen and Webster, 1986b). Sodium acetate stimulated the germination of ascospores of *Chaetomium thermophile* var. *coprophile* (Celerin and Fergus, 1971), *Sordaria fimicola* (Bretzloff, 1954) and *Sporormiella* spp. (Asina et al., 1977a). Asina and co-workers suggest that *Sporormiella* requires an external energy source for germination and could use acetate as the sole source of energy.

The mechanism by which heat triggers the germination of ascospores under the influence of internal regulatory mechanisms ("constitutive dormancy"; Sussman, 1965) is not fully understood. To induce germination in *Pilobolus crystallinus* and *Podospora tetraspora*, spores were simply heat-treated at 60°C for 10–15 min. (Kuthubutheen and Webster, 1986b). Wicklow and Zak (1979) reported substantial ascospore germination

for *Sporormiella pilosella*, *Saccobolus globuliferellus*, *Podospora glutinans*, and *Podospora curvicolla* on water agar following heat-activation (55–70°C / 60 sec.). Heat activation of ascospores by grassland fires provides an alternative to gut passage for initiating fungal vegetative growth and ascocarp development in coprophilous Ascomycetes (Wicklow, 1975). The restriction of carbonicolous/coprophilous Ascomycetes to burned sites results from their inability to compete successfully in unburned soil (El-Abyad and Webster, 1968; Wicklow and Zak, 1979; Zak and Wicklow, 1980; Wicklow, 1988a).

Fungal growth in dung is affected by the degree of aeration or anaerobiosis, with early colonization of the non-porous dung center prevented by high substrate moisture levels (400–700% dry weight) and limited oxygen (Dickinson and Underhay, 1977). Even so, *Sporomiella minima* has been grown under near anaerobic conditions (Brewer et al., 1972). Dung insects indirectly modify the physical environment for fungal/microbial growth by churning the dung center. Arthropod mixing increased bacterial and yeast productivity possibly by continuously exposing individuals to fresh substrate (Lussenhop et al., 1980). At the same time, mixing prevents mycelial networks from becoming established (Breymeyer et al., 1975; Lussenhop et al., 1980). The expansion of hyphal networks into the center of drying dung has been illustrated by Dickinson an Underhay (1977) who recorded densities similar to those observed by Lussenhop et al. (1980). Dung insects leave tunnels that aerate the dung center and reduce microenvironmental extremes (Lussenhop et al., 1980). I find it curious that fungal colonists of cattle dung do not show a yeast-mycelial dimorphism. Fungi having such an adaptation could grow in the fluid dung center, as a yeast, switching to mycelial outgrowth when the dung hardens.

SUCCESSION OF FUNGAL FRUIT BODIES

In their classic paper, Harper and Webster (1964) showed that the time required for production of mature fungal fruit bodies on rabbit dung did not vary when individual fungi were grown alone or in combination with other fungi. Even so, for fungal species colonizing more than one dung type the earliest date of fruiting may vary (Lodha, 1974). Prior to the work by Harper and Webster it was generally believed that the activities of earlier colonists, in depleting substrate nutrient reserves, influenced patterns of growth and sporulation among later fruiting species (Burges, 1958; Garrett, 1956). We now recognize that while white-rot Basidiomycetes can enzymatically attack recalcitrant lignocellulosic residues (Wicklow et al., 1980b; 1980c), Basidiomycetes are not necessarily the last to fruit on dung (Larsen, 1971; Lodha, 1974; Wicklow and Moore, 1974). Fungi whose vegetative development is delayed until after the activity of other microbes has ceased, or those fungi requiring a prolonged period of vegetative development before they can sporulate, could become extinct in habitats where dung rapidly disappears before such sporocarps are formed (Wicklow, 1981a). This may explain why the interval of fungal fruit body appearance on dung from the tropics is shorter than that for dung collected in temperate latitudes (Lodha, 1974). In semiarid grasslands, the slow rate of decomposition of cattle dung results in the accumulation of different aged dung pats, each supporting a characteristic assemblage of fungal colonists (Angel and Wicklow, 1983; Wicklow and Angel, 1983). Fungal communities associated with a particular age class of dung (fresh dried, 6, 18, 30, or 54 months) were most similar to those communities on dung samples nearest in age. Furthermore, the numbers of fungal species recorded from dung were similar throughout the 54-month period of field expo-

sure. This indicates that some of the earlier appearing (fruiting) species are replaced by later fruiting species. *Podospora anserina* was common on freshly dried cattle dung but was not recorded from aged dung (Angel and Wicklow, 1983). This fungus undergoes a lethal senescence, growth becoming transformed from a 'juvenile' to a 'differentiated' state (Benne and Tabak, 1986; Rayner and Coates, 1986). It is difficult to explain the selective advantage of lethal senescence in *Podospora anserina* (Schulte et al., 1988) and *Podospora curvicolla* (Bockelmann and Esser, 1986). Is indeterminate growth, with the potential for repeated fruiting, disadvantageous? At the same time, does *Pilaria anomala* in some way benefit from maintaining metabolic activity and continuing to degrade the coprome days after sporulation had ceased (Wood and Cooke, 1987).

The influence of water availability on the succession of fungal fruit bodies on rabbit dung was studied by Kuthubutheen and Webster (1986a). The order of appearance of fungal fruit bodies on aged dung, incubated with free water in the laboratory, was similar to that observed using fresh dung pellets. The largest number of fungal species was recorded from dung pellets provided with free water, and only four of 29 species of Ascomycetes produced mature ascocarps at humidities below 100% Kuthubutheen and Webster (1986a) discovered that most Deuteromycetes (20/25 species) could fruit at subsaturated atmospheres (98% - 81% r.h.) but not on dung incubated with free water. Spores of *Podospora crystallinus*, *Podospora tetraspora* and *Saccobolus versicolor* failed to germinate and mycelial growth did not occur at or below 0.94 A_w, but *Sporormiella intermedia* spores germinated and mycelia grew very slowly at 0.92 A_w (Kuthubutheen and Webster, 1986b). Dickinson and Underhay (1977) also reported that fewer fungi produced fruit bodies on dung when the moisture content was slightly lower than that of fresh dung. With decreasing water availability there was a decrease in both mycelial growth rate and in the minimum fruiting time for *Pilaira anomala* and *Sordaria humana* (Harrower and Nagy, 1979). The authors propose that by reproducing earlier, these fungi increase the chance of dispersal before growth is arrested. Kuthubutheen and Webster (1986b) present evidence that coprophilous fungi may be able to survive periods of protracted drought as mycelia with arrested growth.

Some species of coprophilous fungi are adapted to different segments of a moisture gradient. When dung pellets from rabbits fed sterile hay inoculated with either *Sporormiella intermedia*, *Saccobolus versicolor* or *Podospora tetraspora* were incubated at reduced humidities, these fungi sporulated on pellets incubated over the range of FW - 92% r.h. (Kuthubutheen and Webster, 1986b). However, when fed with 10 other species, these fungi showed a reduced ability to fruit at lower r.h. The "other species" included *Onychophora coprophila*, *Doratomyces nanus* and *Isaria felina*, which showed more abundant fruiting at reduced moistures than with FW. The authors note that in the presence of competitors, the production of synnemata of *Doratomyces nanus* was not affected but fruiting of *Onychophora coprophila* was limited to lower humidities. This work offers an excellent example of how the realized niche of an organism is shaped by competitors.

Temperature influences the composition of coprophilous fungal communities on rabbit dung and order of fruit body appearance (Wicklow and Moore, 1974; Kuthubutheen and Webster, 1986a). There was a general relationship between the rate of weight loss (Angel and Wicklow, 1974) and the time required for certain coprophilous fungal populations to produce sporocarps on dung (Wicklow and Moore, 1974). Daily fluctuation of temperatures during the growing season in temperate ecosystems may explain why psychrophilic species such as *Thelebolus* (Wicklow and Malloch, 1971) can be found fruiting alongside species with higher temperature optima on the same dung collection (Wicklow and Moore, 1974).

The effects of exposure to light on the development of coprophilous fungi colonizing deer dung in Japan was examined by Morinaga et al. (1980). Successional pattern of fruiting was altered from that seen in the field when dung pellets were incubated in continuous light or darkness. Fruiting of *Pilobolus crystallinus*, *Lasiobolus cuniculi*, *Saccobolus* sp. and *Gyrothrix* sp. appeared to be stimulated by light. Light versus dark incubation had no impact on the growth or fruiting of *Sordaria fimicola* or *Sporormiella* spp. in laboratory culture media (Hawker, 1966; Asina et al., 1977b). There have been numerous other reports on the role of light in stimulating fruit body formation for fungi that are known to colonize dung.

MICROCLIMATE, HABITAT, AND SEASON

Climatic factors, vegetational cover, and soil properties will determine temperature and moisture relations in dung and therefore indirectly regulate metabolic activities and competitive abilities of potential fungal colonists. The importance of habitat-related microclimate in determining the structure and composition of fungal communities was demonstrated by Yocom and Wicklow (1980). Dung pellets from rabbits fed from the same bale of hay were exposed on the soil surface of different habitats within a dune succession. Fungal community structure and composition differed substantially in response to both the habitat in which samples were exposed as well as climatic patterns unique to each exposure interval. Yocom and Wicklow (1980) observed a linear relationship between the amount of precipitation and the numbers of fungal species appearing on rabbit dung. Moisture availability also appears to be the most important factor in determining fungal community composition in North American prairie ecosystems (Angel and Wicklow, 1975; 1983). A distinct and predictable seasonal cycle of fruiting is reported for the fungal flora on dung of the brush-tailed opossum *(Trichosurus vulpecula)* in New Zealand (Bell, 1975). Maximum numbers of fungal species fruited in wet winter months (June-August) and minimum numbers in warm, drier summer months. This suggests that the arboreal opossum is consuming the spores of a greater variety of coprophilous fungi with its winter diet than with its summer diet. Dickinson and Underhay (1977) note that in spring and fall the water content of dung falls slowly, whereas in summer it declines dramatically in a very short time. Fewer fungi can fruit successfully and discharge spores from dung surfaces that have rapidly dried. Booth (1977) conducted the most comprehensive ecosystem-level study on the effects of climate and microhabitat on fungal fruiting and dung decomposition, including estimates of dung contributions of minerals and organic substances in high Arctic tundra ecosystems. Booth characterized dung as a "non-random nutrient hot point."

FUNGAL INTERACTIONS

Coprophilous fungi must compete for substrate volume and for space on the dung surface to produce fruit bodies critical to their dispersal. In both plant and animal populations, intraspecific competition related to high initial colonization densities could be expected to have an adverse effect on the population. In principle, individual germlings of the same vegetative compatibility group may avoid the negative effects of intraspecific competition through hyphal anastamosis (Wicklow, 1981a). In practice anastomoses are likely to be curtailed by the simultaneous infection of substrates by numerous clones which show vegetative incompatibility. Interference competition

results in a reduction in sporocarp numbers among coprophilous fungi (Harper and Webster, 1964; Ikediugwu and Webster, 1970; Safar and Cooke, 1988b). Kuthubutheen and Webster (1986a) observed that when 11 fungi representative of the various phases of the typical succession were fed simultaneously to caged laboratory rabbits, fruit bodies of all the species were observed, but the numbers of fruit-bodies each species produced represented only a fraction of those counted when each fungus was present singly in the dung. These results imply that direct interference or exploitative competition is occurring. Bell (1975) reported a 42% occurrence of *Streptomyces* spp. on dung from the brush-tailed opossum. Few fungal fruit bodies were observed on fecal pellets colonized by *Streptomyces* spp. Safar and Cooke (1988a) present evidence suggesting that bacteria may ameliorate fungal antagonism in dung. The addition of bacteria to copromes enabled certain competitively inferior fungal colonists to produce fruit bodies. Wicklow and Yocom (1981) found that when species were combined in dung, decomposition losses never exceeded the lower value recorded for any of the species grown singly. Likewise, resource use by coprophilous fungi did not increase when the number of species in the dung pellets was increased (Lussenhop and Wicklow, 1985). The authors suggest that because the spores of coprophilous fungi land on vegetation by chance there is little opportunity for efficient resource partitioning in dung. Surprisingly, the competitive dominant on the basis of numbers of spores produced, did not necessarily cause the most weight loss and there was no connection between spore number and hyphal biomass (Lussenhop and Wicklow, 1985). Others have found, however, that in radiation sterilized copromes, species mixtures often produce higher degradation rates than those effected by a single species (Wood and Cooke, 1987; Safar and Cooke, 1988b). It should be noted that sterilized compromes represent somewhat contrived microcosms which may differ from natural dung samples in a number of respects; consequently, these results should be interpreted with caution.

Our research on the distribution of antagonistic fungi in a coprophilous fungal succession on cattle dung (Wicklow and Hirschfield, 1979; Angel and Wicklow, 1983) suggested that the antagonistic properties of fungi and their ecological status in a successional community (i.e. competitive hierarchy) are predictable and this information may be exploited in developing effective strategies for biological control or in guiding a search for novel antifungal antibiotics (Wicklow, 1981b). Wicklow and Hirschfield (1979) described a competitive hierarchy among coprophilous fungal species. *Poronia punctata*, a late colonist of cattle dung, exhibits antagonism towards several of its natural competitors in vitro. *Poronia* produces an antifungal metabolite which inhibits the growth of *Sordaria fimicola* and *Ascobolus furfuraceus*, two early-occurring dung colonists. The major antagonistic component was isolated from culture filtrates of *Poronia punctata* in large quantities and was identified as (+)-isoepoxydon (Gloer and Truckenbrod, 1988). (+)-isoepoxydon has been implicated as an intermediate in the biosynthesis of patulin, a mycotoxin produced by *Penicillium* spp., but no patulin was detected in cultures of *Poronia punctata*. Assays of isoepoxydon for activity against the test organisms showed symptoms of hyphal damage identical to those observed in assays for direct competition between *Poronia punctata* and the test organisms. Furthermore, plugs of cattle dung agar medium were cut from zones uninvaded by the test organisms after assays for direct competition. Analysis of extracts of the plugs by TLC and HPLC confirmed the presence of isoepoxydon as a major component. *Podospora decipiens*, an early colonist that continues to sporulate on aged cattle dung (54 months field exposure), produced podosporin A, a new tetracyclic sesquiterpene quinone that exhibited

antifungal activity to *Sordaria* and *Ascobolus* (Weber et al., 1988). Fungi whose position in the successional sere is less well documented, *Preussia fleischhakii* and *Preussia isomera* also produced novel metabolites with activity against *Sordaria* and *Ascobolus* (Weber and Gloer, 1988; Weber et al., 1990).

Noncompetitive limiting factors may keep populations below the size at which competition plays an important role. Wicklow and Yocom (1982) wanted to learn if arthropod predation promotes fungal diversity in coprophilous communities. They found that sciarid fly larvae *(Lycoriella mali)* at all treatment levels suppressed the number of fungal species found fruiting on rabbit dung. In a related study, numbers of larvae surviving to pupate rose with additions of fungal species to the community, resulting in greater overall decomposition losses (Lussenhop and Wicklow, 1985).

Greater numbers and kinds of arthropods were attracted to 0-day-old dung samples than to fecal pellets on which coprophilous fungi had fruited in the laboratory before field exposure (Helsel and Wicklow, 1978). Only *Ptenothrix unicolor* was isolated in consistently greater numbers from the laboratory incubated dung. Fungal colonization of dung undoubtedly alters the kinds of 'dung volatiles' produced and the subsequent attraction of dung insects. The fetid, dung-like odors emitted by some mushrooms are believed to have attracted the dung beetles found colonizing decaying mushrooms (Bornemissza, 1971). Sciarid larvae *(Lycoriella auripila)* preferred unspawned manure compost containing no mycelium, larval survival being impaired in spawned compost that was heavily colonized by mushroom mycelium (Binns, 1975). Sciarid larvae *(Lycoriella mali)* avoided ascocarps of *Chaetomium bostrycodes* that had fruited on rabbit dung but consumed the fruit bodies of coexisting fungi (Helsel and Wicklow, 1978). This suggested that *Chaetomium bostrycodes* has effective mechanical and chemical defenses against fungus-feeding arthropods (Wicklow, 1979; 1988b). Antiinsectan chemicals have also been reported from *Aspergillus leporis* sclerotia that form naturally on rabbit dung (Wicklow, 1985; Tepaske et al., 1991). There is no evidence that mycoparasitism is an important factor in structuring fungal communities on dung, although, *Piptocephalis* reduced growth and sporulation of *Pilaira anomala* when grown in agar culture but not on herbivore dung (Wood and Cooke, 1986).

DECOMPOSITION PROCESSES

Successional pattern on cattle dung is correlated with fungal efficiency in scavenging cellulose from the digested remains of grasses (Wicklow et al., 1980b). *Hypocopra merdaria* and *Poronia punctata*, two slow-growing and late successional Ascomycetes, were more effective in degrading the cellulose in wheat straw than earlier fruiting species. Angel and Wicklow (1983) made the interesting observation that cattle dung of different ages up to 54 months, decomposed at equivalent rates. This suggests that the fungal community on older dung pats can efficiently degrade a more recalcitrant substrate. Coprome decomposition rates were greater when fungi were paired with bacteria than when single fungal species were acting alone (Safar and Cooke, 1988a). Fungal bacteriolysis causes the disintegration of bacterial cells and may be important in fungal colonization of dung and in nutrient cycling. For example, the cultivated mushroom *Agaricus bisporus* and other fungi isolated from a mushroom compost are capable of using bacterial cells as their sole carbon and nitrogen source (Fermor and Wood, 1981). *Agaricus bisporus* produced extracellular bacteriolytic enzymes when grown on media containing heat-killed cells of *Bacillus subtilis* (Grant et al., 1984). Coprophilous Myxomycetes

are also presumed to feed on bacteria and other microorganisms in dung (Eliasson and Lundqvist, 1979).

Basidiomycetes colonizing ruminant dung in grassland ecosystems represent the ecological equivalents of wood white-rot fungi (Wicklow et al., 1980b). Lignin-degrading, white-rot Basidiomycetes can facilitate the decomposition of cattle feces by freeing cellulosics to enzymatic digestion by other coprophilous fungi (Wicklow et al., 1980b). Saito (1966) had shown earlier that, during the breakdown of beech litter, partially decomposed beech leaves are colonized by late-arriving Hymenomycetes such as *Collybia* spp. or *Mycena* spp. This results not only in a rapid decomposition of the leaves but also improving the nutritional status of the substrate so that it can support the growth of subordinate "soft-rot" or "brown rot" microfungi. At the same time, leaf litter exudates consisting of phenolic condensates generated by the oxidative degradation of lignin can inhibit fungal endocellulase and beta-glucosidase (Sinsabaugh and Linkins, 1987). Whether lignin degradation products inhibit fungal enzymes in decomposing dung is not known. A strain of *Cyathus stercoreus* isolated from cattle dung effected substantial losses in lignin from wheat straw during fermentation and efficiently metabolized the degradation products of lignin from wheat straw (Wicklow et al., 1984; Abbott et al., 1984). Low-molecular-weight nonvolatile materials constituted less than 5% of the total ^{14}C lignin released from labeled lignin by *Cyathus stercoreus* (Abbott et al., 1983). The majority of the water-soluble biodegradation products (89%) are lignin-carbohydrate complexes with molecular weights greater than 1000. The primary gas resulting from lignin breakdown and metabolism was CO_2 (Abbott et al., 1983). The rationale for selecting *Cyathus stercoreus* in attempting to modify biologically the lignin and cellulose of wheat straw or other gramineous agricultural residues was based on the expectation that this organism is ecologically specialized to attack enzymatically the substructures of native lignins in grasses. Natural lignins of grasses are known to differ from those of other plant taxa in the relative frequency of certain chemical substructures. Undigested lignocellulose is a principal component of cattle dung in grasslands.

Nutrient nitrogen (N) suppressed lignocellulose degradation for the typical white-rot fungi of woody substrates, *Pleurotus ostreatus* and *Phanerochaete chrysosporium*, but not a coprophilous Basidiomycete isolated from cattle dung (Freer and Detroy, 1982). Nitrogen fertilization of semiarid rangeland increased dung nitrogen concentration and the rate of cattle dung decomposition (Lussenhop et al., 1982). With many fungi, the synthesis of a large number of enzymes and permeases involved in nitrogen metabolism are subject to repression by preferred nitrogen sources, especially ammonium and L-glutamine. The C/N ratio of wood (200:1; Levi and Cowling, 1969) differs considerably from that of cattle feces (16:1 to 26:1; Angel and Wicklow, 1983). White-rot fungi isolated from woody substrates with limited N degrade lignin best under limited N environments (Freer and Detroy, 1982).

TECHNOLOGY TRANSFER OF ECOLOGICAL DATA

Coprophilous fungi have been recognized for attributes of potential value to the fermentation industry (Wicklow, 1989). Companies seeking to screen novel sources of fungal germplasm should benefit from knowledge of the naturally occurring compounds that activate spores of coprophilous Ascomycetes and other fungi (Asina et al., 1977a; Furuya and Naito, 1980). Such chemicals can be applied in the isolation of new or infrequently recorded fungal species from soil or plant litter.

Because several medically important fungi such as *Pseudallescheria boydii*, the causative agent of inflammatory tumors or mycetoma, are common colonists of cattle manure (Bell, 1976), coprophilous fungi represent a relevant source of germplasm to screen for metabolites with specific antifungal activity (Wicklow, 1989). For example, *Sporormiella affinis* produces a major dichlorinated metabolite with antifungal activity against a keratinophilic dermatophyte, *Microsporum gypseum* (McGahren et al., 1969). Keratinophilic dermatophytes (e.g. *Trichophyton terrestre*, *Chrysosporium keratinophilum* and *Chrysosporium pruinosum*) were isolated routinely from samples of cattle, horse, sheep and goat dung (Dominik and Majchrowicz, 1970; Caretta et al., 1976). Might some coprophilous fungi be sources of natural antiinsectan chemicals for use in controlling *Lycoriella mali* infestations of commercial mushroom compost (Cantelo, 1979). Nematode trapping fungi have been incorporated into cattle dung to control a dung-inhabiting parasitic nematode that infects grazing calves (Gronvold et al., 1989). White-rot Basidiomycetes that colonize dung can biologically degrade lignocellulose, even with the addition of nutrient nitrogen (Freer and Detroy, 1982). This information offers fermentation microbiologists greater latitude in applying nutrient nitrogen to promote mycelial growth without suppressing delignification.

SUMMARY

The dung microcosm provides experimental options for the ecologist that cannot be reproduced without disturbing the habitat or the natural biotic community. In nature the dung 'islands' colonized by coprophilous fungi will eventually 'sink' as they decompose and become mixed into the soil by invertebrates. The reproductive success (fitness) of a coprophilous fungus can be measured by its ability to escape from the island in the form of spores. Counts of fungal sporocarps on dung surfaces provide a meaningful measure of how factors such as incubation temperature, competition or predation impact fungal fitness. Patterns of fungal sporocarp development and estimates of total fungal biomass can be recorded against a background of decomposition losses and changes in the chemical composition of dung. Coprophilous fungi represent a relevant source of antifungal antibiotics and offer fermentation microbiologists a source of 'white-rot' fungi that can efficiently degrade lignocellulose in the presence of nutrient nitrogen.

REFERENCES

Abbott, T. P., James, C., and Plattner, R. D. (1983). Products of wheat straw biodegradation by *Cyathus stercoreus*. In *Unconventional Sources of Dietary Fiber*, I. Furda (Ed.). ACS Symposium series, No. 214, pp. 267–284.

Abbott, T. P. and Wicklow, D. T. (1984). Degradation of lignin by *Cyathus* species. *Appl. Environ. Microbiol. 47*: 585–587.

Abdullah, S. K. (1982). Coprophilous mycoflora on different dung types in southern desert of Iraq. *Sydowia/Ann. Mycol. 35*: 1–5.

Angel, K. and Wicklow, D. T. (1974). Decomposition of rabbit feces: an indication of the significance of the coprophilous microflora in energy flow schemes. *J. Ecol. 62*: 429–437.

Angel, K. and Wicklow, D. T. (1975). Relationships between coprophilous fungi and fecal substrates in a Colorado grassland. *Mycologia 67*: 63–74.

Angel, K. and Wicklow, D. T. (1983). Coprophilous fungal communities in semiarid to mesic grasslands. *Can. J. Bot. 61*: 594–602.

Anson, A. E., Fisher, P. J. and Kuthubutheen, A. J. (1985). Interactions between *Pilobolus crystallinus* and *Pseudomonas paucimobilis* isolated from rabbit dung. *Trans. Brit. Mycol. Soc. 85*: 161–164.

Asina, S., Jain, K., and Cain, R. F. (1977a). Factors influencing ascospore germination in three species of *Sporormiella*. *Can. J. Bot. 55*: 1908–1914.

Asina, S., Jain, K., and Cain, R. F. (1977b). Factors influencing growth and ascocarp production in three species of *Sporormiella*. *Can. J. Bot. 55*: 1915–1925.

Bell, A. (1975). Fungal succession on dung of the brush-tailed opossum in New Zealand. *New Zeal. J. Bot. 13*: 437–462.

Bell, R. G. (1976). The development in beef cattle manure of *Petriellidium boydii* (Shear) Malloch, a potential pathogen for man and cattle. *Can. J. Microbiol. 22*: 552–556.

Benne, R. and Tabak, H. F. (1986). Senescence comes of age. *Trends in Genetics 2*: 147–148.

Binns, E. S. (1975). Mushroom mycelium and compost substrates in relation to the survival of the larvae of the sciarid *Lycoriella auripila*. *Ann. Appl. Biol. 80*: 1–15.

Bistis, G. N. and Raper, J. R. (1963). Heterothallism and sexuality in *Ascobolus stercorarius*. *Amer. J. Bot. 50*: 880–891.

Bockelmann, B. and Esser, K. (1986). Plasmids of mitochondrial origin in senescent mycelium of *Podospora curvicolla*. *Curr. Gen. 10*: 803–810.

Booth, T. (1977). Muskox dung: its turnover rate and possible role on Truelove Lowland. In *Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem*, L. C. Bliss (Ed.). Univ. of Alberta Press, Edmonton, pp. 531–545.

Bornemissza, G. F. (1971). Mycetophagous breeding in the Australian dung beetle, *Onthophagus dunningi*. *Pedobiologia 11*: 133–142.

Bretzloff, C. W. (1954). The growth and fruiting of *Sordaria fimicola*. *Am. J. Bot. 41*: 58–67.

Brewer, D., Duncan, J. M., Safe, S., and Taylor, A. (1972). Ovine ill-thrift in Nova Scotia. IV. The survival at low oxygen partial pressure of fungi isolated from the contents of the ovine rumen. *Can. J. Microbiol. 18*: 119–128.

Breymeyer, A., Jakubczyk, H., and Olechowicz, E. (1975). Influence of coprophilous arthropods on microorganisms in sheep feces—laboratory investigations. *Bull. Acad. Pol. Sci. 23*: 257–262.

Burges, A. (1958). *Micro-organisms in the soil*. Hutchinson, London.

Cantelo, W. W. (1979). *Lycoriella mali*: control in mushroom compost by incorporation of insecticides into compost. *J. Econ. Entomol. 72*: 703–705.

Caretta, G., Del Frate, G., Piontelli, E., Todaro, F. (1976). Microflora cheratinofila del pelo e dello sterco di mucca, del foraggio e del suolo di fattoria: considerazioni sulla loro distribuzione. *Rivista Parassitol. 37*: 333–361.

Celerin, E. M. and Fergus, C. L. (1971). Effects of nutrients, temperature and relative humidity on germination and longevity of the ascospores of *Chaetomium thermophile* var. *coprophile*. *Mycologia 63*: 1030–1045.

Dickinson, C. H., and Underhay, V. H. S. (1977). Growth of fungi in cattle dung. *Trans. Brit. Mycol. Soc. 69*: 473–477.

Dominik, T. and Majchrowicz, I. (1970). Further contribution to the knowledge of keratinolytic and keratinophilic fungi of the region of Szczecin-keratinolytic and keratinophilic fungi in excrements of farm animals. *Ekol. Pol. 18*: 571–611.

El-Abyad, M. S. H., and Webster, J. (1968). Studies on pyrophilous discomycetes. II. Competition. *Trans. Brit. Mycol. Soc. 51*: 369–375.

El-Ani, A. S. and Olive, L. S. (1962). The induction of balanced heterothallism in *Sordaria fimicola*. *Proc. Nat. Acad. Sci. (Wash.) 48*: 17–19.

Eliasson, U. and Lundqvist, N. (1979). Fimicolous myxomycetes. *Bot. Notiser 132*: 551–568.

Esser, K. and Straub, J. (1958). Genetische Untersuchungen an *Sordaria macrospora* Auersw., Kompensation und Induktion bei genbedingten Entwicklungsdefekten. *Z. Vererbungsl. 89*: 729–746.

Fermor, T. R. and Wood, D. A. (1981). Degradation of bacteria by *Agaricus bisporus* and other fungi. *J. Gen. Microbiol. 126*: 377–387.

Freer, S. N. and Detroy, R. W. (1982). Biological delignification of ^{14}C-labeled lignocelluloses by Basidiomycetes: degradation and solubilization of the lignin and cellulose components. *Mycologia 74*: 943–951.

Furuya, K., and Naito, A. (1980). Stimulation of ascospore germination by phenolic compounds in members of the Sordariaceae. *Trans. Mycol. Soc. Japan 21*: 77–85.

Garrett, S. D. (1956). *Biology of Root-Infecting Fungi*. Cambridge Univ. Press, New York.

Gloer, J. B. and Truckenbrod, S. M. (1988). Interference competition among coprophilous fungi: Production of (+)-isoepoxydon by *Poronia punctata*. *Appl. Environ. Microbiol. 54*: 861–864.

Grant, W. D., Fermor, T. R. and Wood, D. A. (1984). Production of bacteriolytic enzymes and degradation of bacterial cell walls during growth of *Agaricus bisporus* on *Bacillus subtilis*. *J. Gen. Microbiol. 130*: 761–769.

Gronvold, J., Henriksen, S. A., Nansen, P., Wolstrup, J., Thylin, ostertagi (Trichostrongylidae) in grazing calves by adding mycelium of the nematode-trapping fungus *Arthrobotrys oligospora* (Hyphomycetes) to cow pats. *J. Helminthol. 63*: 115–126.

Harper, J. E. and Webster, J. (1964). An experimental analysis of the coprophilous fungal succession. *Trans. Brit. Mycol. Soc. 47*: 511–530.

Harrower, K. M. and Nagy, L. A. (1979). Effects of nutrients and water stress on growth and sporulation of coprophilous fungi. *Trans. Brit. Mycol. Soc. 72*: 459–462.

Hawker, L. E. (1966). Environmental influence on reproduction. In *The Fungi*. Vol. II. G. C. Ainsworth and A. S. Sussman (Eds.). Academic Press, New York, pp. 435–465.

Helsel, E. D. and Wicklow, D. T. (1978). Arthropod colonization of pre-aged as compared with fresh feces. *Can. Entomol. 110*: 217–222.

Hesseltine, C. W., Whitehill, A. R., Pidacks, C., Tenhagen, M., Bohonus, M., Hutchings, B. L., Williams, J. H. (1953). Coprogen, a new growth factor present in dung required by *Piloholus*. *Mycologia 45*: 7–19.

Ikediugwu, F. E. O., and Webster, J. (1970). Antagonism between *Coprinus heptemerus* and other coprophilous fungi. *Trans. Brit. Mycol. Soc. 54*: 181–204.

Kuthubutheen, A. J. and Webster, J. (1986a). Water availability and the coprophilous fungus succession. *Trans. Brit. Mycol. Soc. 86*: 63–76.

Kuthubutheen, A. J. and Webster, J. (1986b). Effects of water availability on germination, growth and sporulation of coprophilous fungi. *Trans. Brit. Mycol. Soc. 86*: 77–91.

Lachance, A., Starmer, W. T., and Phaff, H. J. (1988). Identification of yeasts found in decaying cactus tissue. *Can. J. Microbiol. 34*: 1025–1036.

Larsen, K. (1971). Danish endocoprophilous fungi and their sequence of occurrence. *Bot. Tidsskr. 66*: 1–32.

Levi, M. P., and Cowling, E. B. (1969). Role of nitrogen in wood deterioration. VII. Physiological adaptation of wood-destroying and other fungi to substrates deficient in nitrogen. *Phytopathology 59*: 460–468.

Lodha, B. C. (1974). Decomposition of digested litter. In *Biology of Plant Litter Decomposition* I., C. H. Dickinson and G. J. F. Pugh (Eds.). Academic Press, New York, pp. 213–241.

Lu, B. C. (1964). Polyploidy in the Basidiomycete *Cyathus stercoreus*. *Am. J. Bot. 51*: 343–347.

Lundqvist, N. (1972). Nordic Sordariaceae s. lato. *Symb. Bot. Upsal. 20*: 1–374.

Lussenhop, J., Kumar, R., Wicklow, D. T., and Lloyd, J. E. (1980). Insect effects on bacteria and fungi in cattle dung. *Oikos 34*: 54–58.

Lussenhop, J. and Wicklow, D. T. (1985). Interaction of competing fungi with fly larvae. *Microb. Ecol. 11*: 175–182.

Lussenhop, J., Wicklow, D. T., Kumar, R., and Lloyd, J. E. (1982). Increasing the rate of cattle dung decomposition by nitrogen fertilization. *J. Range Manag. 35*: 249–250.

May, G. (1988). Somatic incompatibility and individualism in the coprophilous basidiomycete *Coprinus cinereus*. *Trans. Brit. Mycol. Soc. 91*: 443–451.

McGahren, W. J., van den Hende, J. H., and Mitscher, L. A. (1969). Chlorinated cyclopentenone fungitoxic metabolites from the fungus, *Sporormia affinis*. *J. Am. Chem. Soc. 91*: 157–162.

Meinhardt, F., Koch, H., and Esser, K. (1984). Compatibility groups in *Ascobolus immersus*-an indication of speciation. *Theor. Appl. Genet. 68*: 365–367.

Mitchell, D. T. (1970). Fungus succession on dung of South African ostrich and Angora goat. *J. S. Afr. Bot. 36*: 191–198.

Morinaga, T., Ito, S., and Minoura, K. (1980). Fungal succession on deer dung. The effects of light on the development of certain fungi. *Trans. Mycol. Soc. Japan 21*: 351–357.

Morinaga, T., Tanaka, M., and Minoura, K. (1981). Stimulation of spore germination in *Pilobolus crystallinus* by broth filtrate. *Trans. Mycol. Soc. Japan 22*: 277–282.

Pidacks, C., Whitehill, A. R., Preuss, L. M., Hesseltine, C. W., Bohonos, N. and Williams, J. H. (1953). Coprogen, the isolation of a new growth factor required by *Pilobolus* species. *J. Amer. Chem. Soc. 75*: 6064–6065.

Rayner, A. D. M. and Coates, D. (1986). Regulation of mycelial organization and responses. In *Evolutionary Biology of the Fungi*, A. D. M. Rayner, C. M. Brasier and D. Moore (Eds.). Cambridge Univ. Press, Cambridge, UK, pp. 115–136.

Richardson, M. J. (1972). Coprophilous ascomycetes on different dung types. *Trans. Brit. Mycol. Soc. 58*: 37–48.

Safar, H. M. and Cooke, R. C. (1988a). Interactions between bacteria and coprophilous Ascomycotina and a *Coprinus* species on agar and in copromes. *Trans. Brit. Mycol. Soc. 91*: 73–80.

Safar, H. M. and Cooke, R. C. (1988b). Exploitation of faecal resource units by coprophilous Ascomycotina. *Trans. Brit. Mycol. Soc. 90*: 593–599.

Saito, T. (1966). Sequential pattern of decomposition of beech litter with special reference to microbial succession. *Ecol. Rev. 16*: 245–254.

Schulte, E., Kuck, U. and Esser, K. (1988). Extrachromosomal mutants from *Podospora anserina*: permanent vegetative growth in spite of multiple recombination events in the mitochondrial genome. *Mol. Gen. Genet. 211*: 342–349.

Singh, N. and Webster, J. (1976). Effects of dung extracts on the fruiting of *Pilobolus* species. *Trans. Brit. Mycol. Soc. 67*: 377–379.

Sinsabaugh, R. L. and Linkins, A. E. (1987). Inhibition of the *Trichoderma viride* cellulase complex by leaf litter extracts. *Soil Biol. Biochem. 19*: 719–725.

Starmer, W. T., Phaff, H. J., Miranda, M., Miller, M. W., and Heed, W. B. (1982). The yeast flora associated with the decaying stems of columnar cacti and *Drosophila* in North America, In *Evolutionary Biology*, Vol. 14, M. K. Hecht, B. Wallace and C. T. Prance (Eds.). Plenum, New York, pp. 269–295.

Sussman, A. S. (1965). Dormancy of soil microorganisms in relation to survival. In *Ecology of Soil-borne Plant Pathogens: Prelude to Biological Control*, K. F. Baker and W. C. Snyder (Eds.). Univ. Calif. Press, Berkeley, pp. 99–110.

TePaske, M. R., Gloer, J. B., Wicklow, D. T., and Dowd, P. F. (1991). Leporin A: An antiinsectan metabolite from the sclerotia of *Aspergillus leporis*. *J. Org. Chem.* (in press)

Weber, H. A., Baenziger, N. C. and Gloer, J. B. (1988). Podosporin A: A novel antifungal metabolite from the coprophilous fungus *Podospora decipiens* (Wint.) Niessl. *J. Org. Chem. 53*: 5457–5460.

Weber, H. A., Baenziger, N. C., and Gloer, J. B. (1990). Structure of Preussomerin A: an unusual new antifungal metabolite from the coprophilous fungus *Preussia isomera*. *J. Am. Chem. Soc. 112*: 6718–6719.

Weber, H. A. and Gloer, J. B. (1988). Interference competition among natural fungal competitors: An antifungal metabolite from the coprophilous fungus *Preussia fleischhakii*. *J. Nat. Products 51*: 879–883.

Webster, J. (1970). Coprophilous fungi. *Trans. Brit. Mycol. Soc. 54*: 161–180.

Wicklow, D. T. (1975). Fire as an environmental cue initiating ascocarp development in a tall grass prairie. *Mycologia 67*: 852–862.

Wicklow, D. T. (1979). Hair ornamentation and predator defense in *Chaetomium*. *Trans. Brit. Mycol. Soc. 72*: 107–110.

Wicklow, D. T. (1981a). The coprophilous fungal community: A mycological system for examining ecological ideas. In *The Fungal Community: Its Organization and Role in the Ecosystem*, D. T. Wicklow and G. C. Carroll (Eds.). Marcel Dekker, New York and Basel, pp. 47–76.

Wicklow, D. T. (1981b). Interference competition and the organization of fungal communities. In *The Fungal Community: Its Organization and Role in the Ecosystem*, D. T. Wicklow and G. C. Carroll (Eds.). Marcel Dekker, New York and Basel, pp. 351–376.

Wicklow, D. T. (1985). *Aspergillus leporis* sclerotia form on rabbit dung. *Mycologia 77*: 531–534.

Wicklow, D. T. (1988a). Parallels in the development of post-fire fungal and herb communities. *Proc. Royal Soc. Edinburgh 94B*: 87–95.

Wicklow, D. T. (1988b). Metabolites in the coevolution of fungal defence systems. In *Coevolution of Fungi with Animals and Plants*, K. A. Pirozynski and D. Hawksworth (Eds.). Academic Press, London, pp. 173–201.

Wicklow, D. T. (1989). Fungal succession: Technology transfer of ecological data. In *Recent Advances in Microbial Ecology*, T. Hattori, Y. Ishida, Y. Maruyama, R. Y. Morita, and A. Uchida (Eds.). Japan Scientific Societies Press, Tokyo, pp. 280–284.

Wicklow, D. T. and Angel, K. (1983). Some reproductive characteristics of coprophilous ascomycetes in three prairie ecosystems. *Mycologia 75*: 1070–1073.

Wicklow, D. T., Angel, K., and Lussenhop, J. (1980a). Fungal community expression in lagomorph versus ruminant feces. *Mycologia 72*: 1015–1021.

Wicklow, D. T., Detroy, R. W., and Adams, S. (1980b). Differential modification of the lignin and cellulose components in wheat straw by fungal colonists of ruminant dung: ecological implications. *Mycologia 72*: 1065–1076.

Wicklow, D. T., Detroy, R. W., and Jessee, B. A. (1980c). Decomposition of lignocellulose by *Cyathus stercoreus* (Schw.) de Toni NRRL 6473, a "white rot" fungus from cattle dung. *Appl. Environ. Microbiol. 40*: 169–170.

Wicklow, D. T. and Hirschfield, B. J. (1979). Evidence of a competitive hierarchy among coprophilous fungal populations. *Can. J. Microbiol. 25*: 855–858.

Wicklow, D. T., Langie, R., Crabtree, S., and Detroy, R. W. (1984). Degradation of lignocellulose in wheat straw versus hardwood by *Cyathus* and related species (Nidulariaceae). *Can. J. Microbiol. 30*: 632–636.

Wicklow, D. T. and Malloch, D. M. (1971). Studies in the genus *Thelebolus*. Temperature optima for growth and ascocarp development. *Mycologia 63*: 118–131.

Wicklow, D. T. and Moore, V. (1974). Effect of incubation temperature on the coprophilous fungal succession. *Trans. Brit. Mycol. Soc. 62*: 411–415.

Wicklow, D. T. and Yocom, D. H. (1981). Fungal species numbers and decomposition of rabbit faeces. *Trans. Brit. Mycol. Soc. 76*: 29–32.

Wicklow, D. T. and Yocom, D. H. (1982). Effect of larval grazing by *Lycoriella mali* (Diptera: Sciaridae) on species abundance of coprophilous fungi. *Trans. Brit. Mycol. Soc. 78*: 29–32.

Wicklow, D. T. and Zak, J. C. (1979). Ascospore germination of carbonicolous ascomycetes in fungistatic soils: an ecological interpretation. *Mycologia 71*: 238–242.

Wood, S. N. and Cooke, R. C. (1986). Effect of *Piptocephalis* species on growth and sporulation of *Pilaira anomala*. *Trans. Brit. Mycol. Soc. 86*: 672–674.

Wood, S. N. and Cooke, R. C. (1987). Nutritional competence of *Pilaira anomala* in relation to exploitation of faecal resource units. *Trans. Brit. Mycol. Soc. 88*: 247–255.

Yocom, D. H. and Wicklow, D. T. (1980). Community differentiation along a dung succession: an experimental approach with coprophilous fungi. *Ecology 61*: 868–880.

Zak, J. C. and Wicklow, D. T. (1980). Structure and composition of a post-fire ascomycete community: role of abiotic and biotic factors. *Can. J. Bot. 58*: 1915–1922.